PSYCHE

A JOURNAL OF ENTOMOLOGY

ESTABLISHED IN 1874

Vol. 59 June, 1952 No. 2

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PSYCHE is published quarterly, the issues appearing in March, June, September, and December. Subscription price, per year, payable in advance: $3.00 to subscribers in the United States; Canadian and foreign subscriptions $3.35. Single copies, 85 cents.

Cheques and remittances should be addressed to Treasurer, Cambridge Entomological Club, Biological Laboratories, Harvard University, Cambridge, Mass.

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The March, 1952, PSYCHE (Vol. 59, No. 1) was mailed August 19, 1952

EATON PRESS INC., WATERTOWN, MASS.

PSYCHE

Vol. 59 June, 1952 No. 2

INHERITANCE OF SOME VARIETAL CHARACTERS IN *CHRYSOPA OCULATA* SAY (NEUROPTERA: CHRYSOPIDAE)*

By William E. Bickley
College Park, Maryland

Varieties of *Chrysopa oculata* Say are distinguished by the degree of darkness of wing veins and by color patterns, chiefly markings on the genae, vertex, and pronotum. Most of the varieties are species synonyms. *C. albicornis* Fitch, which has dark cross veins, and *C. chlorophana* Burm., which has green cross veins, were placed under *C. oculata* Say by Smith (1922). One of several reasons for doing so was the fact that the forms readily cross.

Smith (1932 and 1934) recognized five varieties which have different color patterns on the vertex. In *carei* Smith, spots on the vertex are absent. In *xanthocephala* Fitch there are two black or brown spots in the antennal band or closely connected with it; but if the two spots are not connected with the antennal band the form is called *bipunctata* Fitch. Variety *oculata* Say has four dark spots on the vertex (pl. 5, A). In *illepida* Fitch there are two elongate bands; in other words the spots on each side are fused (pl. 5, B).

When large numbers of *Chrysopa oculata* are examined it is found that some specimens cannot be placed in the recognized categories. A good example is a form in which the vertex has two spots on one side and an elongate band on the other (pl. 5, C). In an attempt to clarify the status of some of the varieties, an investigation was made of the inheritance of some characters upon which varieties are based.

* Scientific Art. No. A357, Contribution No. 2338 of the Maryland Agricultural Experiment Station, Department of Entomology. Dr. Sumner O. Burhoe, Professor of Zoology, University of Maryland aided in interpreting the possible genetic status of the varieties.

Field-collected gravid females were put in separate fruit jars with cheese-cloth coverings, and eggs obtained from them were isolated in one-ounce bottles with absorbent cotton plugs. Larvae were given about a dozen field-collected aphids every day or every other day. Sometimes larvae were fed termite workers. They spun cocoons, pupated, and emerged in the small bottles. Adults lived and reproduced satisfactorily in fruit jars. They were given a few aphids and a little water daily. The average duration of the egg stage was approximately three days and the larval stage, 14 days. Adults usually emerged 14 days after the cocoon was spun.

Two varieties were reared, inbred and inter-bred, namely the common *oculata*, which has four spots on the vertex, and *illepida*, which has two elongate bands on the vertex. Seven *oculata* females of unknown ancestry, some from different localities in Maryland, produced 103 offspring. Of these, 101 or 98% were *oculata*. There were one *illepida* and one *xanthocephala* (a form with only two spots). The progeny of two wild *illepida* females consisted of 83 individuals, 58 of which were *oculata* and 25 of which were *illepida*—respectively 70% and 30%.

Twelve pairs of first generation individuals were mated so that offspring of nearly all possible combinations could be studied. To determine whether or not there was any sex linkage, duplicate crosses were made in which the sexes with given characters were reversed.

Results of second generation pairings are given in Table 1. It is obvious that the genes responsible for *oculata* are more prevalent. This appears to be true not only in the populations reared but also throughout the range of the species. It is unlikely, however, that *oculata* is a dominant character in the Mendelian sense, because of its occurrence in offspring from *illepida* parents. Pairing F as given in the table shows that one pair of *illepida* from an *illepida* female produced 50% *oculata* offspring, indicating that they carried the *oculata* gene. This high percentage fur-

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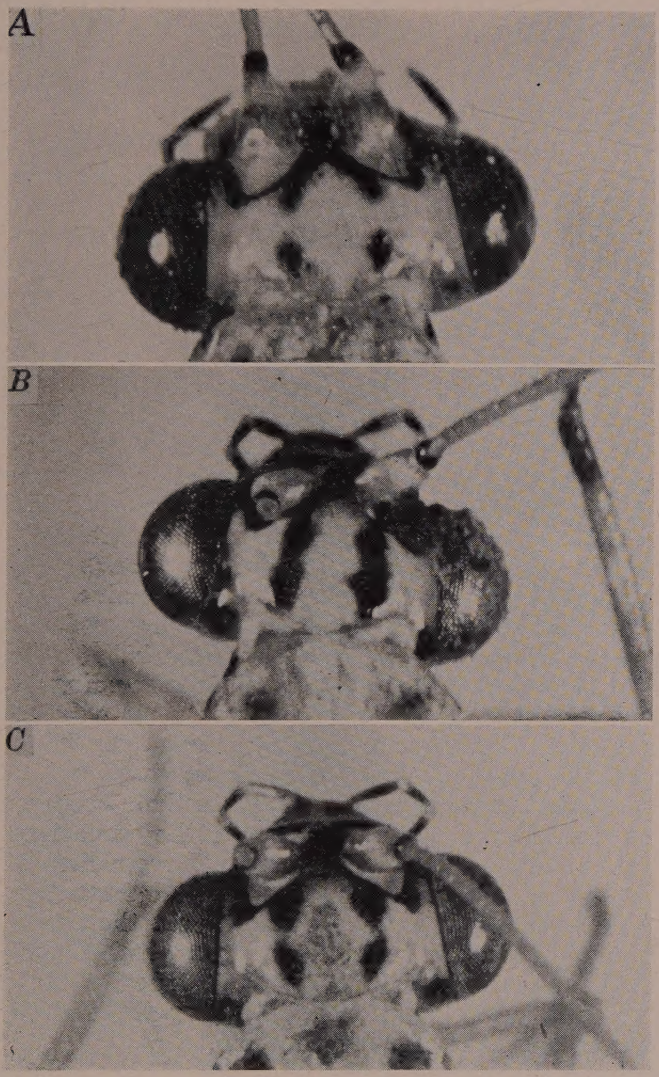
EXPLANATION OF PLATE 4

Markings on the vertex of *Chrysopa oculata*. A. Variety *oculata*. B. Variety *illepida*.. C. "Borderline" individual.



BICKLEY—INHERITANCE IN CHRYSOPA

nishes proof that *oculata* is not a simple dominant. Furthermore, in B, C, and E *oculata*, presumably heterozygous if *illepida* is recessive (because they were the offspring of *illepida* females) produced low percentages of *illepida*. If *oculata* were dominant the expected proportions of *illepida* would be 25% in B and C, and 50% in E.

The high percentage of *oculata* offspring in all the crosses occurs in a manner showing close approximation to the results expected from segregating recessives with a rare production of *illepida*, which could be explained by the presence of two or more pairs of recessive genes either of which in the homozygous recessive state could produce *oculata*. Thus, if there are two genes any one of which in the recessive state would produce *oculata*, a cross like those in D (Table 1) could theoretically produce 25% *illepida*, provided that the *illepida* parent is heterozygous for both pairs of genes. The actual number obtained was 19%. If it is assumed that any one of three genes in the recessive state might produce *oculata*, the actual ratios of the five crosses will conform more closely with the theoretical.

Whatever the genetic mechanism may be, it can be concluded that *illepida* is not a simple recessive. If such were the case, inbreeding could not possibly produce anything except *illepida*, but actually the result is 50% *oculata*. (Table 1, F.) Conversely, the fact that inbreeding of five pairs of *oculata* from an *oculata* female gives only *oculata* suggests that this character may be a recessive. There are of course the other patterns on the vertex to be considered, but no attempt is being made to explain their occurrence.

Even though the manner in which the variations are produced cannot be explained easily and regardless of the percentages of the two varieties obtained from the different crosses, the important point is that the characters which have caused the naming of *oculata* and *illepida* are inherited. Moreover this appears to be true for the other varieties previously mentioned, including those with differences in darkness of wing venation.

An eighth variety recognized by Smith (1932) is *separata* Banks which "is distinguished by the absence of a connection between the black loop under the antennae and the black genal band." If the connection is very faint the

form is still called *separata*. There are various degrees in reduction of width of this connecting band, and in this case it appears that the character is so subtle that it is not reliable.

Because of inconsistencies and intergradations in color patterns and because the genetic status of some of the varietal characters is at least partially understood, it seems reasonable to conclude that the varietal names are no longer of any value. The avoidance of the term variety where it lacks real meaning is one of the principles set forth by Ferris (1928). If this principle is applied the work of the taxonomist will be simplified. He no longer has a problem when he is confronted with borderline cases such as individuals with spots on one side of the vertex and a band on the other, and specimens with the face as in *separata*, the vertex as in *illepida*, and the wings as in *albicornis*.

	Pairing	No. of Pairs	Total Off-Spring	*oculata* No.	*oculata* %	*illepida* No.	*illepida* %	Borderline No.	Borderline %
A	oc(oc) x oc(oc)	5	84	84	100				
B	oc(oc) x oc(ill)	2	83	78	94	4	5	1	1
C	oc(ill) x oc(ill)	1	11	10	91	1	9		
D	oc(oc) x ill(ill)	2	59	48	81	11	19		
E	oc(ill) x ill(ill)	1	60	39	65	21	35		
F	ill(ill) x ill(ill)	1	18	9	50	8	44	1	6

Table 1. Inbreeding and crossing of two varieties of *Chrysopa oculata* (Say); oc(oc) indicates *oculata* from an *oculata* female; oc(ill) indicates *oculata* from an *illepida* female; ill(ill) indicates *illepida* from an *illepida* female.

Summary

Two varieties of *Chrysopa oculata* Say were reared, inbred, and interbred, namely, the common *oculata*, which has four spots on the vertex, and *illepida*, which has two elongate bands on the vertex. Twelve second generation pairings were made and 315 offspring obtained. All of these pairings resulted in high percentages of *oculata*. It is, therefore, concluded that the genes responsible for this character are more prevalent. However, *oculata* is not a

simple dominant, and there is evidence which suggests that there are two or more genes, any one of which in the recessive state produces *oculata*. Because of inconsistencies and intergradations in color patterns and because the genetic status of some of the varietal characters is partially understood, it may be concluded that the varietal names are no longer of any value.

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THE MORPHOLOGY OF THE PROVENTRICULUS OF A FORMICINE ANT

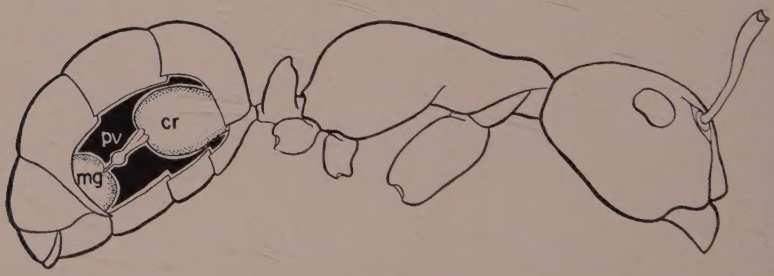
By T. Eisner and E. O. Wilson
Biological Laboratories, Harvard University

The ant proventriculus is a structure of considerable entomological interest. It is most elaborately developed in those groups of ants which have the highest form of social behavior and has been generally thought to be associated in some way with food storage and trophallaxis. It has been used extensively as a taxonomic character in the classification of higher categories in the Dolichoderinae and Formicinae and in phylogenetic speculation concerning these groups. Yet, despite several involved descriptions of the anatomy of this organ that have appeared in the past, its function and activity have never been properly understood. The following paper contains the results of a concentrated study of the morphology of the proventriculus of one typical species of formicine. An emphasis has been laid on those details that appear to be relevant to its function, and there is offered a new explanation of its mechanics.

The first accurate anatomical study of the dolichoderine-formicine proventriculus was that of Forel (1879). Emery (1888) followed up Forel's work in a classic comparative monograph which is still the basic reference on this organ. He reviewed most of the dolichoderine and formicine tribes, as well as the aberrant myrmicine tribe Cephalotini. Additional brief descriptions of the proventriculus of the Dolichoderinae and Formicinae were given in 1912 and 1925, respectively, in the fascicles of Wytsman's *Genera Insectorum* dealing with those groups. The most recent research on the formicine proventriculus is that of Forbes (1938), whose account is mostly a review of earlier work and adds little information of significance.

The ant chosen for the present study was *Camponotus americanus* Mayr. This species proved especially amenable to this type of anatomical work, since it is large and

possesses a translucent integument. The crop, when filled with stained fluid, can be observed through the gastric tergites, so that those individuals that have their crops distended most suitably for dissection can easily be picked from the artificial nests. China ink was found to be the most suitable of several stains considered for use in studying the course of food in the living gut. This was ground up in honey to make an intensely black liquid, which could be traced even when passing through the fine canal system of the proventriculus. Dissections were accomplished simply by clipping the ant's legs, removing the sternites with a fine pair of scissors, picking out the fat body, and washing the cavity of the gaster with insect Ringer's solution. For histological studies the gut was serially sectioned at seven microns and stained with Ehrlich's haemotoxylin and eosin.



Text-figure 1. Soldier of *Camponotus americanus* Mayr, with a window cut in the gaster to show size and placement of the proventriculus. Cr, crop; pv, proventriculus; mg, midgut.

The proventriculus, or gizzard, lies in the anterior half of the gastric cavity when not displaced posteriorly by the distended crop (text--fig. 1.). It is the last segment of the foregut and connects the usually voluminous crop with the midgut. In the "euformicine" ants (section

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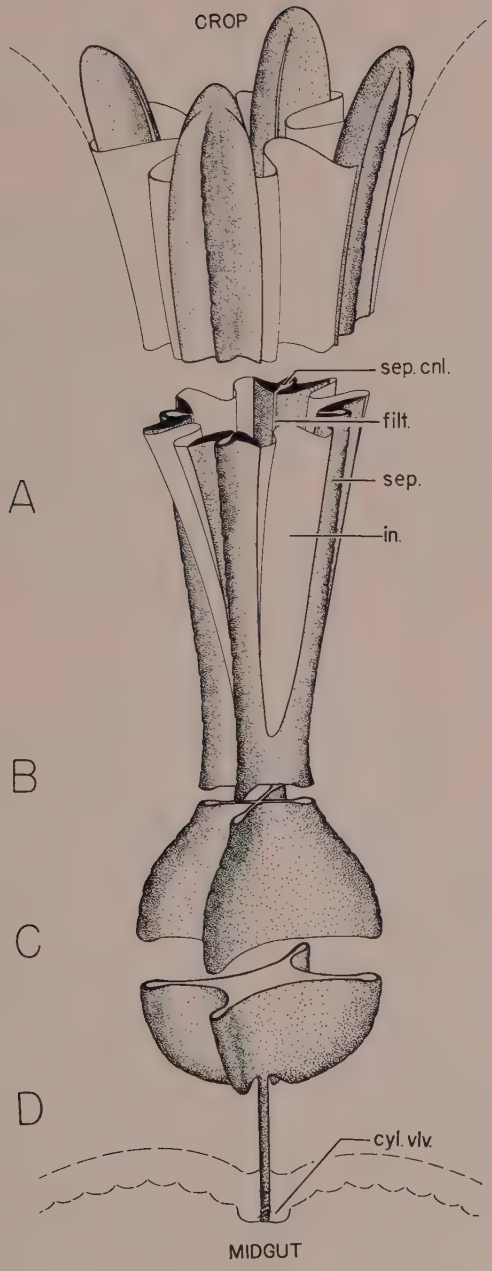
EXPLANATION OF PLATE 5

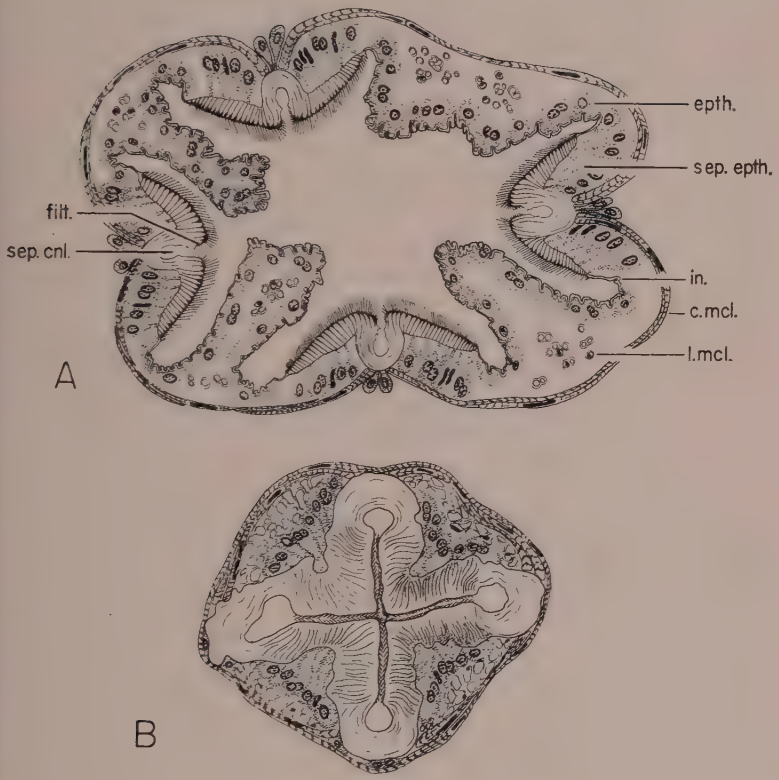
Exploded semidiagrammatic drawing of the chitinous framework of the proventriculus. Epithelium and muscularis not shown. A, calyx; B, occlusory tract; C, bulb; D, cylinder. Sep. cnl., sepal canal; filt., filtering slit of sepal; sep., sepal; in., intersepalary intima; cyl. vlv., cylinder valve. (180X)


CROP
sep. cnl.
filt.
sep.
in.
A
B
C
D
cyl. vlv.
MIDGUT

Euformicinae), under which Emery grouped seven of the twelve formicine tribes recognized by him, and including *Camponotus,* the proventriculus is divided into four distinct parts: the *calyx,* the *occlusory tract* ("valve" of Emery), the *bulb,* and the *cylinder* (pl. 5; A, B, C, D). The calyx is composed of four strap-like, chitinous rods, or *sepals,* which extend anteriorly from the body of the proventriculus to capture part of the posterior wall of the crop. It acts like a collapsible funnel which can be closed by the combined action of its intrinsic muscles and the posterior ring muscles of the crop. Seen in cross-section, each sepal is morphologically differentiated into two zones (plate 6, fig. A), which represent two successive phases of secretion by the underlying epithelial cells. The inner area is composed of closely approximated chitinous hairs, which lend it a finely and evenly striated appearance. The outer zone also appears striate, but coarsely and unevenly so, and it is not composed of independent hairs. This area incloses medially the *sepal canal,* which is to be distinguished from the lateral solid *wings* of the sepal. The canal opens through a narrow slit to the calyx cavity; this slit is a cross section of the longitudinal cleft which extends the full length of the sepal. It is guarded by fine, loosely interdigitating chitinous hairs (collectively designated as the *filter*), which are actually structural hairs of the inner area of the sepal that have been separated from one another. The canal narrows gradually in the anterior end of the sepal and finally ends blindly; it does not extend into the cavity of the crop. The bulk of the calyx wall is made up of epithelium, designated according to position as *sepalary* or *intersepalary.* Externally the wall is limited by a layer of striated muscle, one to two fibers thick, which attaches to the sepals themselves. Between the points of

Explanation of Plate 6

Fig. A, cross section of the calyx at approximately the level of transection shown in plate 6. Fig. B, cross section of the occlusory tract at slightly above the level of transection shown in plate 6. Filt., sepal filter; sep. cnl, sepal canal; epth., intersepalary epithelium; sep. epth., sepalary epithelium; c. mcl., circular muscle fibers; l. mcl., longitudinal muscle fibers. (360X)



EISNER AND WILSON—FORMICINE PROVENTRICULUS

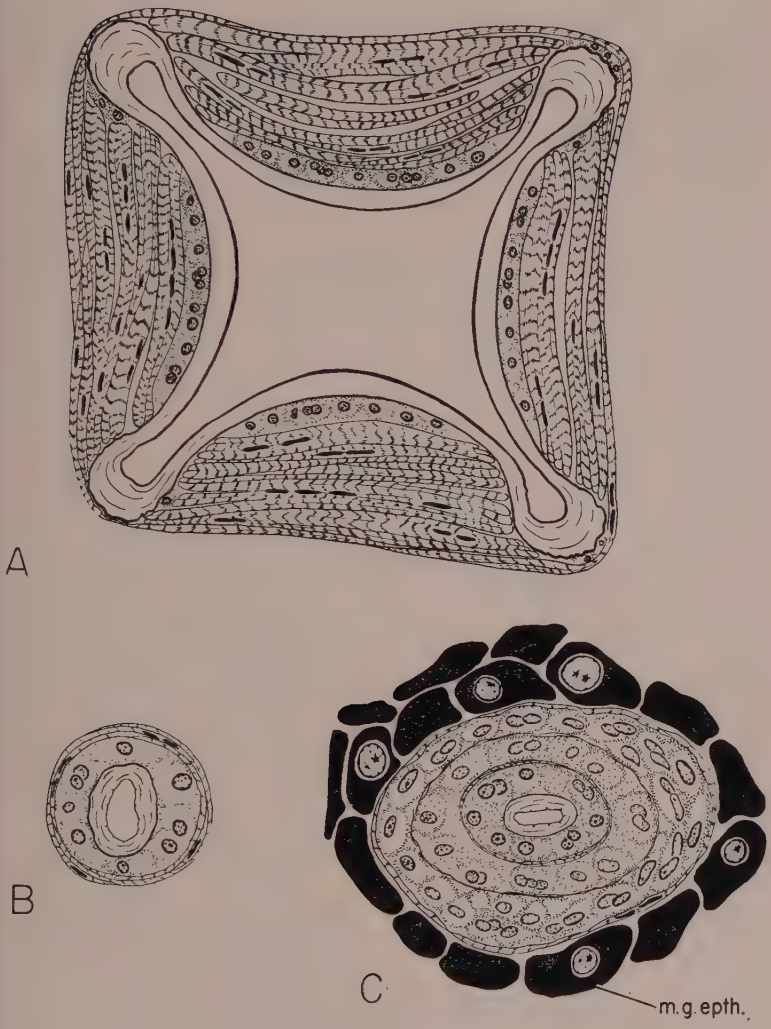
attachment on each sepal is a pair of external epithelioid cells of unknown function. Internally the calyx wall is lined with a chitinous intima, which is continuous with the intima of the crop wall proper. Scattered in the intersepalary folds are slender longitudinal muscle cells; these are few in number and have no obvious function. They are inserted on the anterior face of the bulb and are continuous with the muscularis of the crop.

The occlusory tract, or valve of the previous literature, is formed posteriorly by a coalescence of the sepals in the following manner. As the calyx narrows, the sepals are brought closer together. Their wings shorten, the inner chitinous zone grows progressively thinner, and the outer zone expands toward the center, extending with it the filter area. Finally the inner zone disappears altogether; the sepals curve together and fuse medially. The filter area, seen in cross section of the sepal as a narrow zone separating the canal from the calyx cavity, has now elongated to form one of the filter slits of the occlusory tract (pl. 6, fig. B). The tract is thus a solid chitinous structure having in the center a single united cruciform slit, the arms of which are expanded at their tips into four canals, which are in turn continuous with the sepal canals in front and the bulb canals behind. It is of interest to note here that the arms of the cross are densely covered with chitinous hairs, whereas the canals are bare. The wall of the tract, external to the chitinous cross, is similar to that of the calyx. The longitudinal muscles are more concentrated due to convergence, and the external pairs of epithelioid cells are no longer evident.

The occlusory tract merges into the bulb by a thinning of the intercanal chitin and an expansion of the cruciform slit into the bulb cavity. The outstanding feature of the bulb is the powerful development of its circular muscles, which are five or more fibers thick in cross section.

EXPLANATION OF PLATE 7

Fig. A, cross section of the bulb at approximately the level of transection shown in plate 6. Fig. B, cross section of the cylinder. Fig. C, cross section of the cylinder at the level of the cylinder valve. M. g. epth., midgut epithelium. (360X)



EISNER AND WILSON—FORMICINE PROVENTRICULUS

Longitudinal muscle fibers are absent. Four *bulb canals*, continuous with those of the tract and calyx, extend the length of the bulb and end blindly at the posterior extremity. In the anterior half of the bulb they do not communicate with the bulb cavity, but are closed off by the approximating chitin walls internally adjacent to them. Posteriorly, the walls diverge so that the canals communicate widely with the lumen when the transverse muscles are relaxed (pl. 7, fig. A), but are closed off from the lumen when the muscles contract. As in the calyx and tract, the outer surfaces of the walls form the points of attachment of the transverse muscles.

The bulb merges into the cylinder by a posterior constriction and a termination of the bulb canals. The circular muscles are again reduced to a thickness of one to two fibers, and there is still no evidence of longitudinal muscle fibers (pl. 7, fig. B). Internally the cylinder consists of a simple chitinous tube surrounded by a single-cell layer of epithelium. At its posterior end, as it enters the midgut, the cylinder is seen in our preparations to fold upon itself in such a way as to become a compound tube (pl. 7, fig. C). This is made possible by an extreme thinning of the intima in that area. At the end of the cylinder the intima is folded inside out and back upon the cylinder for a short distance; it is then turned inward again and envelops the cylinder as a third fold before it terminates at the midgut junction. The median intima shown in our figure is therefore actually the true intima folded upon itself. The significance of this rather complicated situation is that the tip of the cylinder is highly flexible, allowing the cylinder to be intruded far into the midgut as the *cylinder valve* ("knob" of previous literature) or to be pulled out of the cavity altogether as a straight, simple tube. Thus the relative lengths of the cylinder and cylinder valve, or those parts outside and inside the midgut cavity respectively, can vary considerably, and the cylinder valve can disappear entirely under some conditions. This phenomenon was first observed by Forel in *Conomyrma pyramica* (1929); we have seen it in several formicine genera, including *Camponotus*, *Lasius*, and *Prenolepis*.

The midgut is of sufficient histological interest to deserve

a note in passing. The wall consists of a loose aggregation of epithelial cells with variably polyploid nuclei. Our method of fixation (Schaudinn's, five minutes) shows a dense concentration of basophilic granules in the cytoplasm. The cells themselves are so loosely connected that they can be dissected out individually with a fine pin, and it seems unlikely that they are able to withstand much pressure from the contents of the lumen.

It has been generally understood that the proventriculus functions in some way to allow storage of liquid in the crop and to regulate the amount which passes into the midgut. This increase in efficiency at storing food in turn facilitates a greater rate of trophallaxis, which is a fundamental bond of social life in higher ants. As to the specific mode of action of this organ, Emery proposed a scheme in his original paper (1888) which to the present time has been varied upon only slightly. This scheme can be summarized as follows. The occlusory tract acts as a valve which is controlled by the muscles surrounding it and which is able to seal off completely the bulb from the crop. In the euformicines the calyx acts as an accessory valve, collapsing its walls together to prevent the flow of liquid through it. The bulb acts as a unidirectional pump with a valve on each end. As the transverse muscles contract, the adjacent walls of the bulb collapse on one another, first at the periphery and then toward the center, forcing the contents of the cavity down through the cylinder and into the midgut. At the same time the occlusory tract closes off independently and prevents flow of the bulb's contents forward into the crop. As the bulb muscles relax, the elasticity of the chitinous wall opens the cavity and creates suction, while the occlusory tract opens and allows liquid from the crop to fill the bulb. The "knob", the end of the cylinder which enters the midgut cavity, acts as a valve to prevent flow of liquid back from the midgut, since its cavity is collapsed by slight external pressure. Regurgitation is initiated by a closure of the occlusory tract (and calyx also in the euformicines) and an expansion of the pharyngeal cavity; the latter process sucks liquid forward out of the crop. This original scheme was based entirely on prepared, sectioned material.

Our studies indicate that while the function attributed to the proventriculus by Emery and others is correct, the accepted explanation of its mechanics as given above is basically erroneous. The reason for this lies in several fundamental misconceptions established by Emery in his 1888 paper and maintained in the literature ever since. First, Emery believed that the filter hairs of the euformicine sepal canals actually seal off the canals from the calyx cavity: "Die Rinne wird gegen das Lumen des Kelches durch das Ineinandergreifen der die Flügel besetzenden Härchen verschlossen". Because of this he was inclined to treat the canals as relatively unimportant structures. Subsequent workers, including Forbes, have observed that the canals really open into the lumen, but none have considered the obvious possibility that they might serve to conduct liquid past the occlusory tract. That this conduction may occur has been ascertained by our observations on the proventriculi of *Camponotus* fed with stained honey. Following spontaneous contractions of the calyx and ejection of the contents into the crop, the canals could often be seen to remain full of the honey, usually back to the level of the occlusory tract, but in one instance through most of the length of the bulb as well. In these cases there were no evidences of the honey in the bulb cavity itself.

A second misconception which Emery established is that the occlusory tract acts as a valve. Actually, even if the occlusory tract could be closed entirely, which is possible, the presence of strongly reinforced canals passing through the tract prevents it from stopping flow altogether. At the same time, the cruciform slit cannot be opened to an extent much greater than that shown in plate 6. In all, the entire structure of the tract appears to be too rigid to be able to exert much control over the rate of flow by the action of its intrinsic muscles.

A third misconception is that the canals of the bulb are collapsed as the transverse muscles contract. We have already seen that these canals are sealed off in the anterior portion of the bulb even when the muscles are relaxed. It is probable that they become sealed off but not collapsed in the posterior portion as contraction is initiated. Why this happens can be seen in an examination of the cross

section of the bulb (pl. 7). The walls of the canals are constructed along their outer edges of exceptionally thick chitin, which cannot easily be folded in. The action of the transverse muscles is obviously to decrease the volume of the bulb. The first thing that must occur as this constriction begins is that the opposing chitinous walls immediately adjacent to the canals meet, although the canals themselves remain open. The point of contact of the walls now proceeds toward the center of the bulb, until, at the completion of contraction, the bulb cavity is mostly obliterated.

A fourth misconception, not entirely referable to Emery, but partly stemming from other authors such as Janet, is that the crop is a passive organ which functions only as a storage center. Examination of entire and dissected *Camponotus*, the crops of which were distended with stained honey, showed that the crop wall is capable of strong and almost total contraction, which at the very least would suffice for regurgitation by itself. In dissected material the movements were most marked in the posterior ring muscles, but they often proceeded anteriorly to include the entire crop. In fully intact but excited and active individuals the crop, when only slightly distended, could be seen through the body wall to undergo very swift pulsations, forcing almost its entire contents into the forward part of the gut.

Our interpretation of the action of the proventriculus in *Camponotus americanus* is as follows. The calyx and occlusory tract are devices for checking the posterior flow of liquid as fluid pressure builds up in the crop. They are able to do this without muscle contraction, simply because more pressure is required to force liquid through the filtering slits than is present even when the crop is considerably distended. Muscle action can have little effect on the width of these filtering slits and therefore cannot exert a valve-like control *per se*. In the euformicines the muscularis can act as a secondary damming device by closing the calyx and preventing liquid from reaching the filtering slits. But in dissected individuals with distended crops the closure of the calyx was not a necessary device, and liquid from the crop failed to reach the bulb even when the calyx was open and its cavity filled. The pressure re-

quired for passing liquid through the calyx and tract is provided by the bulb. As the bulb starts its contraction, its four canals are sealed off, perhaps imperfectly in the posterior portion, but at least completely enough to act as a valve to prevent most of its contents from flowing back into the calyx lumen. As the bulb cavity collapses under muscle contraction, the contents are forced back through the cylinder and into the midgut. As the muscles relax and the cavity expands due to the elasticity of its chitinous framework, the canals of the posterior portion communicate again with the lumen and allow liquid from the anterior canal system to pour in. Probably some of the liquid is sucked in through the filtering slits of the occlusory tract also, but the body of the tract is so extensive and its walls so densely covered with hairs that traffic through it must be relatively insignificant. A forward flow of liquid from the midgut is prevented by the cylinder valve, the thin walls of which can collapse under external pressure.

As we presently understand it, the significance of the characteristic elaboration of the dolichoderine-formicine proventriculus is that it allows the crop to store large amounts of liquid. As previous authors have suggested, it regulates the amount of this liquid which passes into the midgut and in this way separates the individual supply of food from the communal supply. In the concept presented here, it is considered that the primary feature of the advanced proventriculus is the filter area, while the other structures are developed supplementarily. This area acts as a plug guarding the midgut, and liquid can be forced past it only under pressure from the bulb. As its name implies, it also acts as a very thorough filter, and perhaps correlated with this is the fact that the midgut wall is so constructed as to be able to handle only small amounts of pure liquid.

The calyx of the euformicines represents an extension of the occlusory tract which allows a greater filtering area and possibly provides a secondary valvular control by its ability to collapse and occlude liquid from its lumen. In non-euformicine types the calyx is either absent or does not function in this capacity, and the occlusory tract is more massive. In the section Alloformicinae of Emery (Melo-

phorini, Plagiolepidini, and Myrmelachistini), the occlusory tract is a prominent dome which surmounts the bulb. It is traversed by the same cruciform slit found in the euformicines. Anteriorly the slit is covered by dense chitinous hairs; this area is exactly comparable, if not homologous, to the filtered slits of the euformicine calyx and tract. Posteriorly the slit is devoid of hairs, and the tips of its arms broaden into canals which open into the bulb canals, again very much as in the euformicines. The proventriculus characterising Emery's section Heteroformicinae (Myrmecorhynchini and Myrmoteratini) appear from Emery's figures to be essentially similar to the alloformicine type, and there seems to be little justification for considering them other than aberrant alloformicines. The advanced dolichoderine type of proventriculus (Tapinomini) is the most complicated and difficult to understand, but in essential details it is still similar to the alloformicine type. There is an anterior filter area and posterior canals. Sepals, or sepal-like structures, are present and reflexed back over the bulb, with which they fuse. The chitinous septa produced by the fusion of the bulb and inverted sepals serve as the points of attachment of the bulb musculatis. The proventriculus of the myrmicine tribe Cephalotini has unquestionably evolved independently of that of the Dolichoderinae and Formicinae. Yet here again an occlusory tract abuts the crop and is the principal feature. The filtering slits are irregularly branched; they open into a rather simplified muscular portion which is little different from the primitive proventriculus of other myrmicines.

We wish to express our thanks to Dr. A. B. Dawson and Dr. W. L. Brown for critically reading the manuscript and offering many helpful suggestions.

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THE BIOLOGY OF NEARCTIC LEPIDOPTERA
I. FOODPLANTS AND LIFE-HISTORIES OF COLORADO PAPILIONOIDEA

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In recent years the impact of evolutionary studies on taxonomy has greatly enhanced the interest in pairs or groups of species the members of which are almost indistinguishable according to the usual taxonomic criteria but which show no tendency to interbreed in nature and which differ in at least one important environmental specialization. For these Mayr (1940) has coined the convenient term "sibling species". In the Lepidoptera many instances have been discovered in which the siblings differ most strikingly in having special foodplant requirements, the food of each being unacceptable to the other (*e.g.*, Thorpe, 1928; Berger & Fontaine, 1947-48; Rawson & Ziegler, 1950). Some of these situations have been known for many years, and the siblings were formerly characterized as "foodplant races" of a single species.

The exposure of these unrecognized sympatric species in the Lepidoptera is very much hampered by the lack of precise knowledge of the species of foodplants on which each species can develop successfully. By such "success" we ultimately refer to the plant species on which the larvae of the insect will feed readily without fatalities from nutritional failure or from poisoning and on which they can develop to adulthood with normal fertility and inclination to mate. Several instances are now well understood in which: a) females occasionally oviposit on plants on which the larvae cannot thrive; b) larvae appear to prosper on a given plant, but very high losses occur through failure to pupate successfully; c) larvae seemingly develop normally on a given plant, producing adults as usual, but the adults of one or both sexes show no inclination to mate and are apparently sterile. But for most species this precise information is lacking, and even more limiting are the cases in which the food plants are completely unknown.

With the aim of providing some definite information on the foodplants of Lepidoptera I have begun collecting and preserving specimens of the plants, to be submitted to authoritative plant taxonomists for precise determinations. I propose to publish annotated lists of these foodplants from time to time. In the present contribution I have been substantially aided in obtaining plant identifications by my colleague, Dr. John R. Reeder, Curator of the Herbaria at Yale University, and I owe thanks to him and to the determiners: Dr. Reed C. Rollins, Director of the Gray Herbarium at Harvard University; Dr. S. F. Blake, Senior Botanist of the U. S. Division of Plant Exploration and Introductions; and Mr. Carleton R. Ball, of Washington, D. C. Specimens of most of the plants are being preserved for future reference in the Herbarium of Yale University. The initials of the determiner follow each species in brackets. The present paper is devoted to foodplants of Lepidoptera occurring in the state of Colorado. Unfortunately, in the following list little can yet be said about the suitability of the plants as permanent food. Notes on field observations are included. Records of the parasites obtained will be held for future publication.

Papilionidae

1. *Papilio eurymedon* Lucas. On 15 July 1949, J. D. Eff saw a female oviposit on a leaf of *Crataegus rivularis* Nutt. [R.C.R.] on the western slope of Rabbit Ears Pass, in Routt Co., Colo. The larva eclosed on 29 July and was preserved. In California Comstock recorded the foodplant as *Rhamnus californica*. My correspondent there, W. H. Evans, wrote (*in litt.*): "A *Papilio eurymedon* laid four eggs on cultivated jasmine. Each year this species oviposits occasionally on this plant but I have never seen larvae on this vine. This year I gave them tender leaves on which they nibbled for several days, eating just barely enough to keep alive; then I gave them some of the native food plant, *Rhamnus crocea ilicifolia*. But all died without even tasting these leaves."

2. *Parnassius smintheus* Dbldy. & Hew. A single ovum was found 6 July 1949 attached to a leaf of *Oxytropis*

lambertii Pursh. [R.C.R.] near Nederland, Boulder Co., Colo. The ovum was fertile. This appears to be another case of a mistake by an ovipositing female, but there was no opportunity to test the nutritional suitability of *Oxytropis*. The usual foods of *Parnassius* are Crassulaceae, Saxifragaceae, and Papaveraceae. One must question Wright's records of *Viola* and *Vaccinium*. Females of *P. smintheus* from Nederland laid numerous ova on a native *Sedum* in confinement, 11 July 1949. The larvae emerged in the laboratory 12-14 September 1949, although they would normally have overwintered in the egg stage.

Pieridae

3. *Euchloe ausonides* Bdv. During the summer of 1949 larvae and ova were found almost everywhere they were sought in Boulder County at all elevations between 5600′ and 9000′. At Nederland on 6 July several ova and a half-grown larva were taken on *Arabis drummondi* Gray and *Arabis fendleri* (Wats.) Greene var. *spatifolia* (Rydb.) Rollins and one small larva on *Erysimum capitatum* (Dougl.) Greene [all R.C.R.]. The next day, in Spring Gulch, several ova and young larvae and one half-grown larva were taken on *Arabis glabra* (L.) Bernh. [R.C.R.]. This *Arabis* has erect pods, and it was noted that *Euchloe* were absent entirely from a co-occurring and similarly common *Arabis* with decumbent pods (*spatifolia?*—not collected) and from *Erysimum*. At Mt. Flagstaff and 6500′ elevation in Boulder Canyon, on 8 July several large larvae were taken on huge plants of *Sisymbrium altissimum* L. [R.C.R.]. The next day a female *E. ausonides* was observed at Nederland ovipositing on small plants of *S. altissimum* [R.C.R.], and on 22 July several large larvae were found there on the same species of plant. Also on the 22nd, a female was seen laying two ova on *A. fendleri spatifolia*. These two ova were laid in a remarkable manner, being fastened by their sides to flower buds, rather than attached by the base and standing out at right angles to the substratum as is uniformly true of the thousands of other ova I have seen laid by females of a score or more species of Pieridae. It is clear that species of *Arabis* and *Sisym-*

brium are primary foodplants of *E. ausonides* and that the eggs are laid and the larvae feed largely on the flower buds and seed pods. The suitability of other plants as food remains uncertain. The literature on North American Euchloini too often refers simply to "Cruciferae". In Connecticut we have found that the larvae of *Anthocaris midea* (Hbn.) regularly die on some members of the family, even though wild females occasionally oviposit on them.

4. *Pieris rapae* (L.). On 9 July 1949, at Nederland, females were seen ovipositing on *Thlaspi arvense* L. [R.C.R.], and on the 11th a female oviposited on a large *Sisymbrium altissimum* L. [R.C.R.]. The ova were notably white when laid (see *P. protodice,* below). In general, *P. rapae* is still uncommon in the mountains, perhaps in part because it may not thrive on native Cruciferae, and the weedy forms are not very abundant there. In spite of the presence of *P. rapae, P. napi* is by far the commonest *Pieris* above 7000′; it is believed to have been largely extirpated from New England by *P. rapae* (Scudder, 1889, p. 1198). The much greater success of *P. napi* in the Rocky Mountains, where both species oviposit on *Thlaspi* (see *P. napi,* below), suggests that *Thlaspi* may be nutritionally inadequate or poisonous for *P. rapae.*

5. *Pieris protodice* Bdv. & Lec. There is no unanimity in the name for the Colorado population of low and middle altitudes. However, I am satisfied that it cannot be a species distinct from eastern *protodice.* Near and above timberline there is a very striking form (*calyce* Edw.?), which may be a separate species. *P. protodice* females were seen at Nederland on 9 July 1949, ovipositing on *Sisymbrium altissimum* L. [R.C.R.] and *Thlaspi arvense* L. [R.C.R.]. The new ova were distinctly yellowish, contrasting with some of *P. rapae* taken at the same time (see above).

6. *Pieris napi* (L.). On 5 July 1949, at Eldora in Boulder County, Colo., a female was seen laying several ova on tiny seedlings of *Thlaspi arvense* L. [R.C.R.]. The new eggs were white. At Eldora, on 28 July, many *Thlaspi* plants beside a dirt road were examined. Fifty-six ova and a few young larvae of *P. napi* were found. Fifty-one ova

were on the underside of leaves; five were on the lower surface of large seed-silicles. Thirty of these ova were present singly on leaves or silicles; there were two ova on each of twelve leaves and one silicle (once one ovum was laid on top of the other); one leaf bore three ova. It was not possible to determine how often two or three ova were laid at a single visit of a female, but on 5 July I actually saw the female lay two ova side by side on certain leaves. At Rabbit Ears Pass, Routt Co., Colo., on 15 July, Jeanne E. Remington saw a *napi* female lay several ova on *Arabis drummondi* Gray [R.C.R.]. In Europe *P. napi* has been reared on plants of at least seven genera of Cruciferae (including *Sisymbrium*), but in Coos Co., New Hampshire, the basic, if not exclusive, food is *Dentaria,* according to information received from Donald J. Lennox.

7. *Colias eurytheme* Bdv. This name is used here for all orange members of the *eurytheme-philodice* complex of North America. The pure yellow individuals (*philodice*) are not common in the mountains in Boulder County, but observations suggest that they are permanent residents and survive the winter up to high altitudes. As the season progresses, huge orange individuals (*eurytheme*) begin to appear and increase in numbers for some weeks. There is clearly some hybridizing with *philodice,* as in all other regions where the two species are sympatric; I have a small series from Boulder County taken in 1949 above 8,000′, which includes two males and one female of *philodice,* three males and eight females of "pure" *eurytheme,* two females which look like my laboratory backcrosses to *eurytheme,* one female like my experimental F_1 hybrids, and three white females not certainly placeable. The determination of foodplants of these two species of *Colias* in any locality is of great interest, so it is regrettable that the following records are so scanty. On 6 July 1949 a "pure" *eurytheme* female was seen ovipositing on *Thermopsis montana* Nutt. [R.C.R.]. Six days later at Nederland a female *eurytheme* laid several ova on the upperside of leaves of an *Astragalus* which Dr. Rollins tentatively identified as *"racemosus* Pursh.?" (fruit was not collected).

SATYRIDAE

8. *Oeneis brucei* (Edw.). A female taken by J. D. Eff at Berthoud Pass (elev. between 11,000′ and 12,000′), Gilpin Co., Colo., was confined 16 July 1949 over a sedge. It oviposited freely at Eldora, at an altitude about 3,000 feet lower than the normal occurrence at Berthoud. The larvae emerged and fed readily, but all died en route to Connecticut or soon after arrival there.

9. *Oeneis lucilla* B. & McD. A female taken at about 13,000′ on Mt. Evans, Clear Creek Co., Colo., was confined over sedge. At Eldora, over 4,000′ lower than the point of capture, this female laid several ova on 29 July 1949. My records do not show whether the ova were fertile; in the collection are four preserved ova but no larvae.

10. *Erebia epipsodea* Butler. On 11 July 1949 females from Eldora were confined, each over a grass and a sedge. In two days 19 ova were laid, nearly all on the grass, but a few on the sedge; the grass was distinctly preferred for oviposition. The ova were fertile.

NYMPHALIDIDAE

11. *Boloria eunomia alticola* (B. & McD.). On 30 July 1949 females were found in fair numbers in a large alpine bog at Caribou (elev. 10,000′), Boulder Co., Colo. Many were followed closely, but they did not seem strongly-inclined to oviposit and, further, the strong wind made it difficult to keep track of a given individual. However, one female was observed ovipositing and the two ova were recovered. The behavior of this female was unlike that of all others (of both sexes) watched. This one alighted on the lowest plants on small hummocks rising a few inches above the standing water of the bog; the others always came to rest on shrubs and the flowers of tall herbs. The ovipositing female crawled for several seconds into the rather thick low plants (largely Graminales and a tiny *Thalictrum*) and stopped twice to oviposit on leaves of *Thalictrum alpinum* L. var. *hebetum* Boiv. [R.C.R.]. The ova were later lost, and captive females did not oviposit,

so the suitability of *Thalictrum* as a foodplant was not tested.

Our knowledge of foodplants for this genus is in a very confused state. A wide spectrum of plants has been recorded (*e.g.*, see Scudder, 1889, p. 587) as foodplants. However, information is lacking as to the plants **on which larvae were successfully reared.** From our experiences with *B. toddi* (Holland) and *B. selene myrina* (Cramer) in Connecticut, we believe that *Viola* spp. are the only suitable foodplants, but a large series of field observations shows that the females of both species characteristically avoid *Viola* for actual oviposition, although in many instances violets were found a few inches away. Most of the ova were fastened to dead twigs and grass! I suspect that most, if not all, of the recorded "foodplants" of *Boloria*, other than *Viola*, actually represent oviposition observations rather than feeding records. It is doubted that *Thalictrum* is the food of *B. eunomia alticola*.

12. *Boloria selene tollandensis* (B. & Benj.). At the type locality, in the great bogs at Tolland, Gilpin Co., Colo., on 22 July 1949 a female under observation laid an ovum on a dead *Salix* twig several inches above the ground and several feet from the nearest living *Salix*. The ovum was preserved before eclosion. I believe that the actual foodplants at Tolland are *Viola* spp. and that this female exhibited the same habit described above for *B. selene myrina* in Connecticut.

13. *Nymphalis milberti* (Godt.). Several clusters of large larvae were found on 9 and 11 July 1949, on extensively defoliated clumps of *Urtica gracilis* Ait. [R.C.R.] growing in a trash dump near Nederland (elev. 8000′), Boulder Co., Colo. On the same plants were single, concealed larvae of *Vanessa atalanta*. On 25 July many larvae of *N. milberti* of all sizes were found on stream-side clumps of *Urtica* at an elevation of 7200′ in Boulder Canyon. In the same clumps were several full-grown larvae of *V. atalanta* and four solitary larvae of *Polygonia satyrus*. Many larvae and pupae of the Nederland *N. milberti* were preserved; the remainder completed development on *U.*

gracilis and emerged during several days beginning on 26 July.

14. *Vanessa atalanta* (L.). Two sites of collection of larvae were mentioned above (see *N. milberti*). In addition a single larva was taken on *Urtica* at Rabbit Ears Pass, Routt Co., Colo., on 15 July 1949. In the Boulder Canyon clumps a pupa of *V. atalanta* was found in one of the webbed-leaf nests characteristic of *V. atalanta*. The larvae of the three *Urtica*-feeding Nymphalididae were easily distinguishable by their habits: *V. atalanta* was always in snug nests and always solitary; *N. milberti* was always gregarious, although the social groups were much subdivided and dispersed toward the end of development; *P. satyrus* constructed at best very simple nests and was not notably gregarious, and in addition the pair of branched head-horns and the broad, creamy dorsal stripe were distinctive. The *V. atalanta* larvae were very heavily parasitized by Larvaevoridae, and four minute Chalcidoidea emerged (as hyperparasites?) from a pupa.

15. *Vanessa cardui* (L.). Many larvae of all sizes were found on *Cirsium undulatum* (Nutt.) Spreng. [R.C.R.] near Spring Gulch, 9 mi. n.w. of Boulder, Colo., on 7 July 1949; two larval webs each contained a dead larva and a cocoon of one of the Ichneumonidae. Females of *V. cardui* were seen on 9 July ovipositing repeatedly on *Artemisia ludovicianus* Nutt. var. *gnaphalodes* (Nutt.) T. & G. [R.C.R.] in clearings in the pine woods near Nederland, Colo. This being an atypical foodplant, special care was taken to be sure that the butterflies were all *V. cardui*, that ova were actually laid, and that the *Artemisia* was always the plant selected. It is not known whether the larvae fed and matured on *A. gnaphalodes*. No thistles were found in these clearings. In 1949 *V. cardui* was unusually numerous in Boulder County as well as elsewhere in North America (see Eff, 1950), and these ovipositing females were probably second generation descendants of immigrants. *V. cardui* appears to oviposit commonly on plants of doubtful adequacy during these great emigrations and then to use only *Cirsium* and other thistles during the

intervening years of much less abundance. In the vicinity of St. Louis, Missouri, I never found larvae of *V. cardui* on anything but thistles except in the years of great influx, but then garden hollyhocks (*Althea rosea* Cav.) were always heavily infested. There is a very long list of recorded foodplants for *V. cardui* in North America and Eurasia, but *Artemisia* seems to be previously unlisted. Careful tests of the whole range of recorded plants for their suitability to *V. cardui* for development would be valuable.

16. *Vanessa virginiensis* (Drury). Several solitary larvae were found on 9 July 1949 in their familiar nests on *Antennaria aprica* Greene [S.F.B.] near Nederland, Colo. This is an uncommon butterfly in the mountains, and its larvae were found more easily than the adults.

17. *Polygonia satyrus* (Edw.). On 25 July 1949 one full-grown and three half-grown larvae were found on streamside *Urtica* (*U. gracilis?*) clumps at an elevation of 7200′ in Boulder Canyon, Colo. These were interspersed with larvae of *Vanessa atalanta* and *Nymphalis milberti* (see above). One larva was allowed to complete development, and the imago emerged on 8 August 1949. From the fact that they are allopatric and from the appearance and foodplant of the larvae I suspect that *P. comma* and *P. satyrus* are actually conspecific; the pattern and color differences of the adults are slight enough.

18. *Limenitis weidemeyerii* Edw. A female was seen laying several ova on the tips of leaves of *Salix* along a stream, at Eldora, Boulder Co., Colo., on 18 July 1949. One ovum laid on *Salix drummondiana* Barratt var. *subcaerulea* (Piper) Ball [C.R.B.] was recovered; the larva emerged on 30 July and was preserved.

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Heteroponera Mayr Reinstated (Hymenoptera: Formicidae). — *Heteroponera* Mayr (1887, Verh. zool.-bot. Ges. Wien, *37*: 533) has remained suppressed as a synonym of *Acanthoponera* Mayr for many years. Wheeler (1923, *loc. cit.*) has shown, however that *Acanthoponera* can be split into two groups; one group (*Acanthoponera* s. str.) having the tarsal claws with an extra, strong tooth and a basal lobe (or tooth), while the second group (*Anacanthoponera* Wheeler) has the tarsal claws at most with a single, weak median tooth. In this second group, Wheeler included *Heteroponera carinifrons* Mayr, and since *Heteroponera*, with the genotype *H. carinifrons*, has precedence, it must be **reinstated as a good genus**. *Anacanthoponera* Wheeler (1923, Psyche, *30*: 176, as a subgenus of *Acanthoponera*) is a **new synonym** of *Heteroponera*, since the genotype, *Ponera dolo* Roger, is congeneric with *H. carinifrons*.

Acanthoponera is neotropical, and has well developed propodeal teeth and the petiolar apex produced as a long tooth or spine; Kusnezov (*in litt.*) finds *A. mucronata* to have 6, 4 palpal segmentation. *Heteroponera* is neotropical and Australasian, and the propodeal teeth and dentiform petiolar apex are absent or feebly developed; *H. imbellis* Emery has 3, 3 palpal segmentation (my dissection). Until more species can be critically examined, *Acanthoponera* and *Heteroponera* should be considered as distinct genera. *Acanthoponera* appears to be the most generalized living member of the Ectatommini, and is probably close to the stem from which the proceratiines, the myrmicines and *Paraponera* arose. — W. L. Brown, Jr., Museum of Comparative Zoology, Harvard University.

STUDIES ON ARIZONA ANTS (3)
THE HABITS OF *POGONOMYRMEX HUACHUCANUS* WHEELER AND A DESCRIPTION OF THE SEXUAL CASTES

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It has been more than a third of a century since Wheeler described *Pogonomyrmex huachucanus* from a few workers taken in the Huachuca Mountains of Arizona (1). During this period only five additional records have been published for this interesting little species. Three of these were carried in Olsen's 1934 monograph on *Pogonomyrmex* (2). The other two records were published by Cole in 1934 (3) and 1937 (4). While these records have increased the known range of *huachucanus,* they have added little to our knowledge of the habits of this insect. There is good indication that *P. huachucanus* has special significance in the phylogeny of the genus *Pogonomyrmex,* hence it is gratifying to be able to amplify our rather meager data on this ant. During the summers of 1950 and 1951 the writer found numerous colonies of *huachucanus* and was able to study some of them in considerable detail. This paper presents the results of these studies, a review of previously published observations on *huachucanus* and a description of each of the three castes.

The nests of *huachucanus* examined by the writer were very uniform in one respect. In every case they were built in extremely harsh, stony soil. The most striking example of this was a nest taken at the summit of Montezuma Pass in the Huachuca Mountains. This nest was constructed in the hard-packed gravel of the highway. Road work had compressed the gravel to such an extent that "soil" around the nest was almost as hard as concrete. Most of the nests were situated on rather steep slopes and they were generally fully exposed to the sun. The direction of the slope seemed to be of little importance. Three of the nests were constructed beneath stones, the others had no covering object present. In the latter case the nest was provided

with a single, rather irregular entrance about one-half an inch in diameter. From this entrance excavated soil was scattered in an obscure fan down the slope. In one instance there was a low crater of excavated soil about six inches in diameter spread around the entrance. But the construction of a crater seems to be exceptional for this species. The population of a nest of *huachucanus* is comparatively small. As a rule there are less than two hundred workers in a colony. The colonies frequently have two or more queens present but this seems to have little effect on their size. One nest, which was secured entire, had only one hundred and seventy workers present although it contained two females. Occasionally one encounters an especially large nest in which four or five hundred workers may be present, but there would seem to be little doubt that such a number is exceptional.

P. huachucanus is not a conspicuously aggressive ant, but it will defend its nest vigorously if disturbed. It has no hesitation about using its sting, but the effect of the sting is remarkably slight, at least to the writer. I have often been stung by half a dozen workers at once, with no results other than a slight twinge as the stings entered. The persistent and distressing after-effects which often accompany the stings of many species of *Pogonomyrmex* seem entirely absent in the case of *huachucanus*.

The marriage flight of *P. huachucanus* takes place in the latter part of July or the first weeks of August. Although the writer has never seen the marriage flight of this species in progress, there is evidence which makes the above statement valid. Mature males were taken from a nest near Socorro, N. M., on July 31st and others from two nests in Carr Canyon, Huachuca Mountains, Arizona, on August 5th. A large nest found near Springerville, Arizona, on July 30th contained not only many males but an equally large number of dealate females. There were far too many of the latter to suppose that they all represented functional females belonging to the nest. As it had rained heavily an hour or two before the nest was discovered, it seems likely that the storm had interrupted a marriage flight and that the dealated females had taken temporary shelter in the nest. It is safe to conclude, therefore, that the marriage flight of

huachucanus, like that of many other species which occur in southern Arizona, takes place during the rainy season of July and August.

We may now consider the distribution of *huachucanus*. Presented below are the previously published locality records for this species and those which the writer secured during 1950 and 1951. The elevation of each of the first thirteen localities has been checked with U.S. Geological Survey topographic sheets. In addition, many of them have been rechecked with an altimeter as well. The last four localities have been checked against data in Stieler's Handatlas.

Huachuca Mountains, Arizona: Miller Canyon 5600′ (Type locality) W. M. Wheeler; Garden Canyon 5800′, W. S. Creighton; Carr Canyon, 5400′, W. S. Creighton; Pyeatt Cave, 5500′, W. S. Creighton; one mile east of Panama Mine, 5300′, W. S. Creighton; Montezuma Pass, 6700′, W. S. Creighton.

Santa Rita Mountains, Arizona: Mouth of Madera Canyon, 4800′, W. S. Creighton; Sweetwater, 5800′, W. S. Creighton.

Santa Catalina Mountains, Arizona:[1] Sabino Basin, 3700′, W. M. Wheeler.

Dragoon Mountains, Arizona: Texas Pass, 4700′, W. M. Wheeler.

Whetstone Mountains, Arizona: Dry Canyon 5000′, W. S. Creighton.

Baboquivari Mountains, Arizona: Brown Canyon 4200-6000′, W. S. Creighton.

Oracle, Arizona, 4500′, W. M. Wheeler.

Seligman, Arizona, 5500′, A. C. Cole.

Springerville, Arizona, 5600′, W. S. Creighton.

Sixteen miles west of Socorro, N. M., 5300′, W. S. Creighton.

Needles, California, 460′, A. C. Cole.

From these records it can be stated that *huachucanus* usually occurs between the 4000 and 6500 foot levels and, since this is the case, it is clear that Dr. Cole's record from Needles is badly out of line in the matter of elevation.

[1] This record is cited as "South Catalina Mountains" in Olsen's monograph.

For it is more than thirty-two hundred feet below the next lowest record for *huachucanus*. The situation and character of the Needles nest were both unusual for a colony of *huachucanus*. Dr. Cole described it as " a rather minute crater mound in sand." It has been shown above that *huachucanus* nests in gravelly soil and only rarely constructs a crater. Since everything about the Needles record is wrong for *huachucanus*, I wrote Dr. Cole for permission to examine the specimens on which it is based. Unfortunately, they have been lost. There is, therefore, no possibility of a further check on this highly unusual record. In my opinion it is best disregarded. It is very unlikely that the ant was actually *huachucanus* and the inclusion of the Needles record obscures the beautifully clear distributional picture which is shown by every other record for *huachucanus*.

For all the other records for this species indicate that *huachucanus* is a member of the Upper Sonoran ant fauna. Many of the records are from mountainous areas and, when the insect occurs in such regions it prefers foothill canyons as nesting sites. It is equally at home, however, on the grassy, elevated plains at the base of the mountains. But it does not occur in nearby areas of less elevation where Lower Sonoran species are encountered. It is interesting to note that, at the eastern end of its range, *huachucanus* occurs in stations where *P. occidentalis* and the typical *P. barbatus* are also present. The main range of the typical *barbatus* lies in Mexico. That of *occidentalis* lies entirely to the north of it as far as is known at present. Hence there is only a limited area in parts of Arizona and New Mexico where these two species occur in close proximity. For the most part the range of *huachucanus* follows this area of overlap with remarkable exactness. The most obvious explanation for the distribution of *huachucanus* would, therefore, assume an unusually narrow tolerance for temperature on the part of this species. Such a limitation would exclude *huachucanus* from northern regions occupied by *occidentalis* and at the same time debar it from southern areas utilized by the typical *barbatus*. If this explanation is correct, then *huachucanus* shows less environmental adaptability than is usually the case with members of the

genus *Pogonomyrmex*. This point is of interest in view of Wheeler's theory that *huachucanus* is a relict species.

According to Wheeler (1) *huachucanus* and the closely allied Chilean species *bispinosus* are the remains of a primitive *Pogonomyrmex* fauna which originated from the genus *Myrmica* in boreal America and subsequently spread southward through the arid portions of both North and South America. This primitive *Pogonomyrmex* fauna was later replaced in large part by more adaptable, modern species. The replacement left relict species at widely isolated points in the orignal range. This theory, which was designed to explain the close structural similarities which mark *huachucanus* and *bispinosus*, was necessarily based upon the characteristics of the worker of *huachucanus*. Wheeler knew nothing of the male of *huachucanus*. The structure of the male is of particular importance in phylogenetic considerations and it is interesting to find that this caste shows features which agree well with Wheeler's view. The general appearance of the male of *huachucanus* is quite unlike that of the males of the other North American species of *Pogonomyrmex*. The latter are good sized insects as ant males go, with a length of nine millimeters or more. This is true even when the worker caste is comparatively small, as is the case with *desertorum*. The surface sculpture is variable but it is never heavy enough to produce a completely dull surface and, in most cases, the body is distinctly shining. The erect body hairs are long, thin, flexuous and very abundant. They often mat together but, even when they do not mat, they are close enough to each other to obscure the parts on which they occur. The antennal scape is at least as long as the first three funicular joints taken together. The male of *huachucanus* is an exception to each of the above features. It is a small insect, not more than seven millimeters long. The sculpture of the head and thorax is dense, giving these parts a dull appearance. The erect body hairs are well separated, stout, evenly curved and notably shorter than those of the other species. They do not mat together nor do they obscure the parts on which they occur. The antennal scape is less than half as long as the first three funicular joints taken together. As to whether these features can be considered primitive is a

debatable point, but it is certainly true that they give to the male of *huachucanus* an appearance which is much more like that of a *Myrmica* male than is usual for a male of *Pogonomyrmex*. It would be interesting to know if the male of *bispinosus* also shows these characteristics. At present this caste appears to be known only from Spinola's original description (5) which is too imperfect to be of much service.

There is one more point that may have a bearing on the primitive status of *huachucanus*. As already noted, several nests of *huachucanus* were excavated to determine their structure. In particular, two of them were completely exposed with all of the passages opened up. I had expected to find stores of seeds in these nests but failed to do so. Yet this species certainly garners seeds, for one occasionally encounters small quantities of chaff on the excavated fans at the nest entrance. It seems possible that the harvesting habit is poorly developed in *huachucanus*, it gathers seeds but it may fail to store them. If true, this would be a further proof of the primitive character of this species. It is to be hoped that additional observations will give us more light on this point. If nests of *huachucanus* can be examined in the fall, winter and spring and not just during the summer months, it should be possible to show the existence of stores of seeds if this ant makes them.

The general features of all three castes of *P. huachucanus* are shown in the figures on Plate 4. The following descriptions deal mainly with details not shown in the above figures.

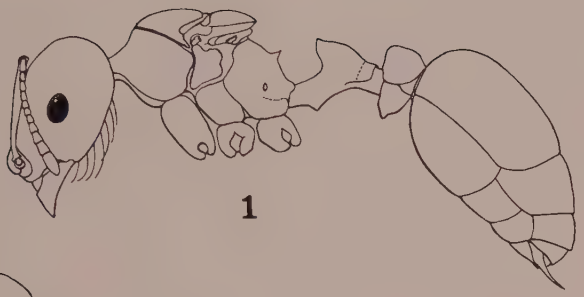
Worker: Length: head (exclusive of the mandibles) 2.25 mm.; thorax 2.75 mm., overall length 5-5.5 mm.

The entire upper surface of the head covered with wavy longitudinal rugae, those at the middle of the head diverging toward the occipital corners. Over most of the upper surface of the head the rugae rarely form reticulations but on the genae and the posterior quarter of the head they are

EXPLANATION TO PLATE 8

Pogonomyrmex huachucanus Wheeler. Fig 1. Female. Fig. 2. Worker. Fig. 3. Male. Fig. 4 Head of female. Fig. 5. Head of worker. Fig. 6. Head of male.

Figs. 1-3 are drawn to the same scale; figs. 4-6 are drawn to the same scale.



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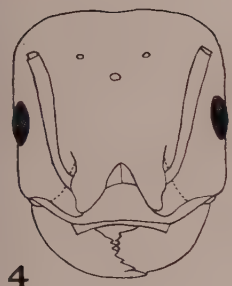

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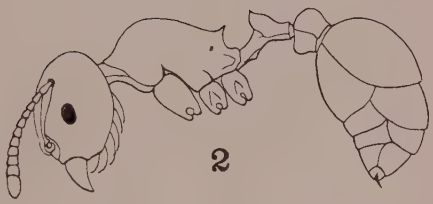

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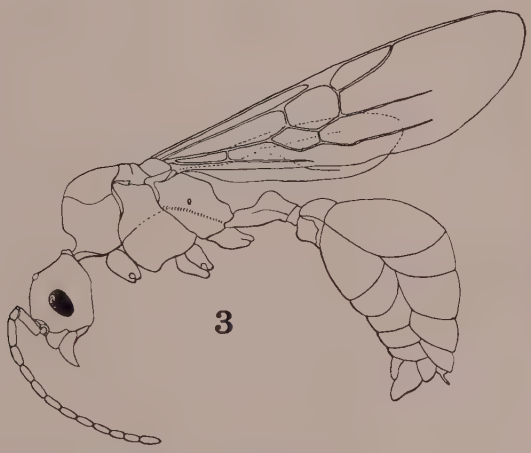

3

6

CREIGHTON—POGONOMYRMEX HUACHUCANUS

distinctly reticulate. The surface between the rugae is densely and minutely granulose with the granules appearing in certain lights as tiny, crater-like rings. The upper surface of the head is dull or very feebly shining except for the anterior ends of the frontal lobes which are rather strongly shining. Mandibles with coarse longitudinal rugae, the surface between the rugae not sculptured, the entire mandible rather strongly shining. Antennal scapes moderately shining with prominent longitudinal rugules.

Thoracic rugae notably reticulate and not parallel on the pronotum. Those on the mesonotum and the mesopleurae also reticulate but with more of a tendency to form roughly parallel, longitudinal ridges. These reticulate rugae turn upward and become transverse on the basal face of the epinotum. The granulate interrugal sculpture of the thorax is more feeble than that of the head and this makes the thorax somewhat more shining than the head. Posterior face of the node of the petiole reticulo-rugose. The interrugal areas, the front of the node and the entire postpetiole densely and finely granulose, dull or at most very feebly shining. Peduncle of the petiole and the coxae with fine punctures which are more widely spaced and do not dull the shining surface. Gaster very strongly shining with minute, widely scattered piligerous punctures. Femora strongly shining with extremely delicate reticulate sculpture. Tibiae more coarsely sculptered and not so strongly shining.

Erect hairs on the upper surface of the head stout, tapered and rather variable in length. Those on the front of the clypeus long and stout, their length equal to that of the longer hairs in the gular ammochaetae. The hairs in the latter structures rather sparse, less than a dozen present at each side of the head. Hairs of the mandibular ammochaetae much shorter and finer than those of the gula. Erect hairs of the thorax very irregular in length, abundant on the promesonotum but sparser on the epinotum, where they are largely confined to an area just behind the mesoepinotal suture. Erect hairs on the petiole and post-petiole very similar to those of the thorax. Erect gastric hairs more uniform in length than those of the thorax, their length increasing gradually from the base of the gaster to

its tip. Antennal scapes, coxae, femora, tibiae and tarsi with numerous, somewhat finer, erect hairs. Erect hairs on the antennal funiculi numerous and fine and grading to pubescence on the terminal segments.

Color: deep ferrugineous red to orange red, the mandibular borders piceous brown. Edge of the first gastric segment often marked with brown.

Female: Length: head (mandibles excluded) 1.75 mm.; thorax 2.25 mm.; overall length 7-7.5 mm.

Cephalic sculpture very similar to that of the worker but with the longitudinal rugae at the center of the head finer and more regular. The interrugal sculpture is less pronounced than in the worker so that the entire head, especially the middle third, is more shining than that of the worker. Mandibles and antennal scapes as in the worker.

Thoracic rugae everywhere coarse and prominent except on the neck of the pronotum and the declivious face of the epinotum. The neck of the pronotum is transversely rugulose at its anterior edge. Behind this rugulose area is a band of dense, though shallow, punctures interspersed with extremely delicate rugules which extends back to the coarse, reticulate rugae on the humeral angles. Rugae of the scutum highly variable. In some specimens transverse, in others longitudinal. Rugae of the scutellum usually longitudinal. Mesothoracic sternite and episternite longitudinally rugose, the rugae turning upward on the sides of the epinotum and becoming transverse on the basal face of the epinotum. Declivious face of the epinotum with two or three feeble, widely spaced rugae. Interrugal sculpture of the thorax like that of the worker but a little more feeble so that the thorax is slightly more shining than that of the worker. Sculpture of the petiolar nodes, gaster and legs like that of the worker.

Erect hairs on the upper surface of the head, thorax, petiolar nodes and gaster slightly more numerous than those of the worker. Erect hairs elsewhere very similar to those of the worker.

Color ferrugineous red, the masticatory margin of the mandibles and the lateral edges of the dorsum of the first gastric segment banded with piceous brown.

Male: Length: head (mandibles excluded) 1.25 mm.; thorax 2 mm.; overall length 6.5-7 mm.

Upper surface of the head with fine, wavy, longitudinal rugae over most of its middle third. These rugae form few reticulations. The rugae of the lateral portions of the head, the occipital angles, the entire occipital border and the gula, notably reticulate. The surface between the rugae dull and densely punctured, the punctures appearing as tiny craters under high magnification. Frontal groove, frontal area and the clypeus slightly shining. Mandibles longitudinally striate and a little more shining than the clypeus.

Entire thorax feebly shining to dull with punctato-rugose sculpture, the punctures very dense. Rugae on the pronotum, mesothoracic sternite and episternite feeble, often replaced by punctures on the front part of the segments. Scutum, paraptera and scutellum with moderately developed, longitudinal, reticulate rugae in addition to the dense punctures. Metathoracic sternite with coarse longitudinal rugae which turn upward on the sides of the epinotum. Basal face of the epinotum with coarse, reticulate rugae. Rugae on the declivious face of the epinotum transverse. Anterior peduncle of the petiole finely punctate and more shining than the remainder of the petiole. The anterior face of the node of the petiole densely and more coarsely punctate. Crest and rear face of the node and the posterior peduncle with reticulate rugae in addition to the punctures. Postpetiole densely punctate but not rugose. Abdomen smooth and shining with extremely fine, scattered, piligerous punctures. Coxal joints, antennal scapes, fore femora and tarsi delicately reticulo-punctate. Middle and hind femora with similar but feebler sculpture.

Erect hairs of moderate length, yellow-brown, evenly curved, tapered and well-separated. Abundant on the dorsum of the thorax, except on the basal face of the epinotum, where they are restricted to the angle between the basal and the declivious faces. Erect hairs on the head about equally numerous on the upper and lower surfaces. Erect hairs on the petiolar nodes notably sparser than those of the thorax. Erect hairs on the gaster very fine, much shorter than those of the thorax and largely limited to the rear edge of each segment. The remaining gastric hairs very

short and usually fully appressed, rarely a few of them suberect. Antennal scapes and funiculi with dense, short, pubescence.

Color: head, thorax, petiolar nodes and femora piceous black. Antennae, toothed border of the mandibles, tibiae and tarsi blackish brown. Gaster clear, golden yellow.

Wings hyaline, iridescent, the veins and stigma brown in some specimens and white in others. The wings evenly covered with small scattered hairs.

The sexual forms were described from nineteen deälated females and forty-nine males taken by the writer at Springerville, Arizona, July 30, 1950.

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AUDIO MIMICRY: AN ADJUNCT TO COLOR MIMICRY

By Albro T. Gaul
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During the summer of 1951, while I was working on some aspects of Vespine wing muscle physiology, I had the opportunity to study some of the wing sounds of certain Vespine mimics. The work was done at Windsor, Mass., with specimens of *Dolichovespula arenaria* F. (Vespidae) and *Spilomyia hamifera* Lw. (Syrphidae). A comparison of the wing tones of these two species has led to the following considerations.

In color pattern, this fly bears a very close resemblance to the wasp, although the abdomen of the fly is somewhat more robust. It is very difficult for me to tell these species apart when they are in flight. Even when the insects are at rest, the longitudinal fuscous band along the wing of the fly makes visual determination difficult without close scrutiny. It is not known just what, if any, function is served by this likeness; nor can it be definitely determined which insect is the mimic and which the model. It is not a unique relationship between the two genera, since *Spilomyia fusca* Lw. closely resembles *Dolichovespula maculata* Linn. in size and color pattern.

The original wing experiments involved the use of a microphone and an electro-mechanical transducer to pick up wing beat tones and thoracic vibrations. The output from these instruments was played through a high fidelity preamplifier and amplifier system and was then led into the input terminals of either an audio-frequency meter or an oscilloscope. With either instrument it was possible to measure the wing-beat frequencies of the insects. A direct comparison of frequencies was therefore made between the wing tones of *S. hamifera* and *D. arenaria*. The more or less standard wing frequency of workers of *arenaria* is

150 strokes per second; while that of *hamifera* is 147 strokes per second. This places both tones between D and D#. These readings were made with 42 *arenaria* workers and 8 *hamifera* adults. The accuracy of the meter was within 1 cycle per second, at this low frequency range. The variation in the wing beats was within plus or minus 2 strokes per second. Temperature is probably not a factor in wing frequency in insects of this size[1].

With the average wing beat differing by only 2 strokes per second, or 1.33%, it is apparent that the average person, including the author, can detect no significant difference in the sounds produced. Even close attention to sound recordings of the two species cannot show any appreciable distinction. It is thus apparent that there is a new form of mimicry, the mimicry of sounds, which in one case at least accompanies color mimicry.

There is little evidence that the color mimicry of these wasps and flies serves any particular function. Perhaps there is common protection against predators, who have only to learn one color pattern. The introduction of sound mimicry into the picture forces us to accept one of two possible conclusions. Either the similarity of wing tone is a chance phenomenon, or we must postulate a significant function to this similarity of wing beats. In the latter case, we should further have to show that certain predators of *Spilomyia* and *Dolichovespula* can detect their prey through sound ranging but are unable to detect the differences which exist between the two sound mimics.

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